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A review of Afrotropical Ctenostylidae (Diptera: Schizophora: ?Tephritoidea), with redescription of *Ramuliseta lindneri* Keiser, 1952

by

D. A. Barraclough

(Natal Museum, P. Bag 9070, Pietermaritzburg, South Africa)

ABSTRACT

The world fauna of Ctenostylidae is briefly reviewed and placement of the family in Tephritoidea discussed; southern African Ctenostylidae are characterised relative to other acalyptrate families. Exclusion of Ctenostylidae from Pyrgotidae is confirmed. Probable plesiomorphic features of Ctenostylidae relative to the ground plan of Tephritoidea are discussed.

The Afrotropical Region has only two known species of Ctenotylidae, one from Madagascar (*Ramuliseta madagascariensis* Hennig, 1960) and the other from southern and east Africa (*R. lindneri* Keiser, 1952). A key to these species is presented, and *lindneri* is redescribed on all available material. The first-instar larva of *lindneri* is described and compared to those known for Ctenostylidae and Pyrgotidae; both Afrotropical species of *Ramuliseta* appear to be larviparous. The first-instar of *lindneri* differs markedly from that of Pyrgotidae in having well-developed mouthhooks and nine anteroventral bands of short spinules. No males of *lindneri* are known, and it is suggested that this species and congeners may reproduce parthenogenetically.

INTRODUCTION

Southern Africa has a rich and diverse fauna of acalyptrate Diptera. The subregion includes some 46 families, one more than the much larger Australian region (see Colless & McAlpine 1991; D. K. McAlpine, *pers. comm.*) and about two less than the entire Neotropical Region (for delineation between Nearctic and Neotropical Regions see Griffiths 1979). Note that I treat the two subfamilies of Aulacigastridae as separate families in accordance with a forthcoming publication by Dr A. Freidberg, and that a new southern and east African family under description by Dr D. McAlpine, Dr A. Freidberg and Dr R. Miller is accounted for. Southern Africa has representatives of a number of small families which have a circumtropical distribution. Two such families, which are particular rarities, are Tachiniscidae and Ctenostylidae, both members of the superfamily Tephritoidea *sensu* Colless & McAlpine (1991). Both families are absent from the Australasian Region, although Ctenostylidae are recorded from nearby Indonesia. Tachiniscidae comprise three named genera and species. The Neotropical genus *Tachinisca* Kertész has been recorded from Brazil, Bolivia, Colombia and Peru (Papavero 1967; J. F. McAlpine 1989). The two Afrotropical genera of Tachiniscidae are *Bibundia* Bischof (central and west Africa) and *Tachiniscidia* (southern, central and west Africa) (Cogan 1980).

The name Ctenotylidae has only recently reappeared in the literature (see D. K. McAlpine 1990), although family status was first accorded to the segregate by Brues & Melander (1932) and Lopes (1935). Previous to McAlpine's publication, Ctenostylidae were usually treated as a subfamily (Lochmostyliinae) of Pyrgotidae. As currently circumscribed (D. K. McAlpine 1990), Ctenostylidae include eight species in five genera. Included genera are: *Tauroscypson* Curran (monotypic, Guyana); *Lochmostylia* Hendel (two species, Costa Rica and Brazil); *Ctenostylum* Macquart (monotypic, ?Brazil); *Furciseta* Aczél (monotypic, Brazil); *Ramuliseta* Keiser (three species, Uganda, Tanzania and South Africa, Madagascar, Indonesia). *Ramuliseta lindneri* Keiser, 1952 is thus the sole known southern African species of Ctenostylidae.

D. K. McAlpine's 1990 arguement that Ctenostylidae are not closely related to Pyrgotidae, and that they cannot be included in any other family of Tephritoidea, is convincing and I agree the group should be given family status. Of particular note is the form of the female terminalia in Ctenostylidae. Tergite 7 and sternite 7 are fused to form a posteriorly tapered tube, and apically a distinct tergite 9 and fused cerci are visible (D. K. McAlpine 1990) (Figs 3 & 5). The tergite 9 and fused cerci are quite unlike those of Pyrgotidae, where apical fusion has produced a heavily sclerotised and sharply pointed aculeus (Fig. 6). The pyrgotid aculeus is used to insert eggs into the abdomen of adult scarabaeid beetles when both fly and beetle are in flight (Ferrar 1987: 304; Steyskal 1987: 814). Such insertion of eggs (or larvae) would not be feasible in Ctenostylidae given the lack of apical piercing structures in the female. None of the ctenostylid eggs I have seen are sharply pointed, and it thus seems unlikely that eggs are thrust through the integument of hosts as in *Stylogaster* species (Conopidae) (Stuckenberg 1963*b*). If the aculeus was present in tephritoids before Pyrgotidae and other families differentiated, as suggested by D. K. McAlpine (1990), then there is a strong case for exclusion of Ctenostylidae from Tephritoidea.

Although Tephritoidea appear at present to be the most appropriate superfamily for placement of Ctenostylidae, a new superfamily may need to be erected to accommodate the family when its affinities are better resolved. A final decision would only be possible when further material, particularly males, becomes available. Examination of *Ramuliseta lindneri* Keiser, 1952, the only known African species of Ctenostylidae, suggests that ctenostylids are in some respects plesiomorphic relative to Tephritoidea. Firstly, the terminalia are less specialised, not being modified to form a rigid, piercing-type ovipositor, this considered to be a tephritoid synapomorphy (J. F. McAlpine 1989). Secondly, although apparently larviparous, the large number of small first-instar larvae counted in dissected specimens of *lindneri* (200–400, see below), coupled with the lack of a rigid ovipositor, possibly suggests that females merely larviposit near areas suitable for larval development, and that first-instar larvae seek out target areas. The anteroventral bands of spinules (see description, below) on the posterior nine segments of the first-instar could assist with such locomotion. All other tephritoids have specific host substrates, either being parasitoids (Pyrgotidae, Tachiniscidae) or generally associated with living or decaying plant matter.

A third character apparent in the Afrotropical species of *Ramuliseta* and which is plesiomorphic relative to the ground plan of Tephritoidea, is the lack of a humeral break, weakening or interruption on the costa. The presence of a humeral break is considered to be an autapomorphy for Tephritoidea by J. F. McAlpine (1989). However, it is also possible that the humeral break or weakening in Ctenostylidae, if accepted as autapomorphic, has been secondarily lost (D. K. McAlpine, *pers. comm.*).

Although very little is known about pyrgotid larvae, the first-instar of the single species recorded by Ferrar (1987: 304) apparently has much reduced mouthhooks, unlike the prominent mouthhooks occurring in the Neotropical ctenostylid *Lochmostylia lopesi* Keiser, 1951 (Ferrar 1987: 304) and both Afrotropical species of *Ramuliseta* (personal observations). Foote (1991) states that pyrgotids have a reduced cephalopharyngeal skeleton as stated by Ferrar, and that ventral welts and spinules are lacking. The well-developed mouthhooks and anteroventral bands of spinules in *Ramuliseta lindneri* are thus atypical of Pyrgotidae and further validate a separate family concept.

A point of exceptional interest is the possibility that *R. lindneri* and congeners are parthenogenetic. *Ramuliseta* is now known from ten localities in the Old World, and all known specimens are female. D. K. McAlpine (1990) refers to a male of *Ramuliseta* from Bwamba Pass (Uganda) seen by G. A. Holloway in The Natural History Museum (London). On a recent visit to this museum, I examined Holloway's Bwamba Pass specimen. It has been damaged by dermestids and almost the entire abdomen is missing. Although I cannot definitely sex the specimen, I believe it is female; both aristae are detached with insertion points visible, thus the suggestion that aristae are lacking in male *Ramuliseta* (D. K. McAlpine 1990: 366) can be refuted. I have dissected the abdomen of *lindneri* females from Tanzania and South Africa, and of *madagascariensis*, and no trace of spermatheca(e), a ventral receptacle or any other form of sperm-storage device could be found. Parthenogenesis is apparently rare in acalyptrates. Cogan (1971) suggests that it occurs in *Prosopantrum flavifrons* (Tonnoir & Malloch, 1927), a species of Heleomyzidae apparently native to South America, but occurring also in New Zealand and South Africa.

RECOGNITION OF SOUTHERN AFRICAN CTENOSTYLIDAE

In southern Africa the Tephritoidea *sensu* Colless & McAlpine (1991) include eight families, namely Lonchaeidae, Piophilidae, Otitidae, Platystomatidae, Pyrgotidae, Tephritidae, Tachiniscidae and Ctenostylidae. Ctenostylidae are distinguished from the other families (and all other acalyptrates in southern Africa) by the simultaneous lack of ocelli and of a functional proboscis (this reduced to a minute vestige, although palpi present). Both these characters are rarely seen in southern African acalyptrates; ocelli are, for example, absent only in Conopinae (the dominant subfamily of Conopidae), all Pyrgotidae and some specimens of *Bromophila caffra* (Macquart, 1846) (Platystomatidae). The arista is dendritically branched in the female; i.e. it never has a single main axis with lateral branches (Fig. 1). This is also an unusual character. The general appearance of *Ramuliseta lindneri* is striking in that the thorax is shortened and rotund, not much longer than head length (Fig. 1). Notable features shared with Pyrgotidae are a great reduction in bristle size, and a reduction in eye size (Fig. 1).

An interesting character found in all *Ramuliseta* species, is that the female has the second basal cell partially open anteriorly (basal half or more of vein 4 absent). D. K.

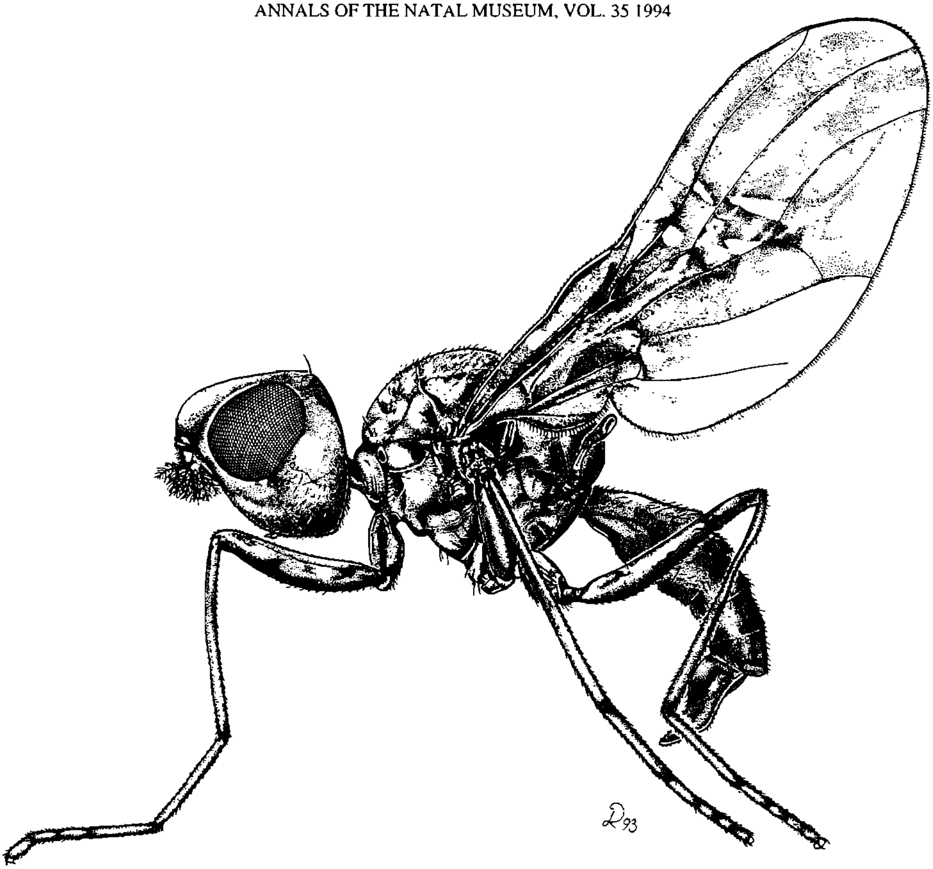


Fig. 1. *Ramuliseta lindneri* Keiser, 1952, lateral habitus of adult female.

McAlpine (1990: 367) incorrectly stated that this vein is complete or nearly so in females of Ctenostylidae. Interestingly, the monotypic genus *Furciseta* Aczél (Brazil), which seems to have closest affinity with *Ramuliseta*, has vein 4 complete in the female according to Hennig (1952: 608), although it is completely lacking in a female from 'Nova Teutonia' I have seen in BMNH. *Furciseta* also differs from *Ramuliseta* in having incurved anterior fronto-orbital bristles (D. K. McAlpine 1990: 369).

MATERIALS AND METHODS

Specimens of *Ramuliseta* examined are all pinned adult females from the following depositories (acronyms in parentheses):

The Natural History Museum, London (BMNH)
Natal Museum, Pietermaritzburg (NMSA)
National Collection of Insects, Plant Protection Research Institute, Pretoria (SANC)
Staatliches Museum für Naturkunde in Stuttgart (SMNS)

Although much of this paper is based on the examination of *Ramuliseta lindneri*, I have also seen in NMSA a single female of *madagascariensis* from southern Madagascar (Lambomakandro, dct (= distr.) Sakaraha, 4–10.ii.1957, B. Stuckenberg, 550 m). The distinction between the two Afrotropical species is confirmed in the key given below; they were considered only weakly separated by Hennig (1960).

Bilaterally symmetrical structures are described in the singular. Holotype label data are quoted exactly as they appear, sometimes with supplementary information in square parentheses; a slash (/) denotes the end of a line of print and a semicolon separates data quoted on different labels. Holotype measurements are given in parentheses following the range for other specimens examined. Body length was measured from the anterior margin of the second antennal segment to the posterior margin of the thorax. Wing length was measured from the humeral crossvein to the wing-tip.

For examination of the female postabdominal region, the entire abdomen was detached at its base. It was then macerated in warm lactic acid (80%), which apparently better preserves membranous structures in small Diptera (Dr T. A. Wheeler, *pers. comm.*). The entire abdomen was stored in glycerine in a microvial pinned beneath each source specimen. Macerated eggs and first-instar larvae were stained to facilitate description, but were not suitable for illustration, storage or mounting.

TAXONOMY

Key to Afrotropical species of *Ramuliseta*

1 Costa with prominent outward flexure prior to subcostal break (Fig. 2). Cells r_{2+3} and r_{4+5} predominantly brown infuscate apically (Fig. 2). [Southern and east Africa.] .... **lindneri** Keiser, 1952

– Costa without outward flexure prior to subcostal break. Cells r_{2+3}, and more noticeably r_{4+5}, hyaline apically. [Madagascar.] .... **madagascariensis** Hennig, 1960

Ramuliseta Keiser, 1951

Ramuliseta Keiser, 1951: 119. Type species: *Ramuliseta palpifera* Keiser, 1951 (Oriental), by original designation.

Ramuliseta lindneri Keiser, 1952

Figs 1–5

Ramuliseta lindneri Keiser, 1952: 325; Aczél, 1956: 34; Hennig, 1960: 326–327; Stuckenberg, 1963*a*: 125–126; Steyskal, 1980: 556.

Holotype: TANZANIA: 'Typus' [red card]; 'Kware [3°22'S:37°12'E] / 17. – 21.I.1952 / D.O.Afrika Exp.' [Blue card]; '*Ramuliseta / lindneri* n.sp. / F. Keiser det.' [Pink card]. In fair condition; abdomen missing and four legs glued to card; ♀ (not ♂ as indicated by Keiser (1952: 325)). In SMNS.

Female: Dimensions (in mm): Head/thorax length 2.5–3.3 (2.8); wing length 3.5–5.1 (3.5).

Colouring/Pollinosity (Fig. 2): Head with yellow ground colour, although apparent coloration dependent on greasiness of specimen and pinkish pigmentation; pollinosity silver and inconspicuous, most noticeable on antenna and face. Frons usually predominantly yellow, but irregularly medium brown in greasy specimens; pinkish pigmentation sometimes apparent on posterior half and narrowly adjacent to eye margins; anterior margin often darker yellow. Lunula often pinkish, either entirely so or particularly along margins. Antenna usually mainly vivid yellow, although dorsobasal section of second segment sometimes slightly darker; irregularly yellow and medium brown in greasy specimens. Facial region and parafacial sometimes irregularly speckled with pinkish pigment, yellow ground colour sometimes darker on either side of mid-facial elevation and/or along epistomal margin. Palpus always yellow. Cheek with anterior section nearly always yellow only; remainder of cheek and lower occipital region usually pinkish pigmented, sometimes strongly so. Occiput always with central part entirely yellow, periphery (upper and lateral margins) usually variably pinkish pigmented. Thoracic ground colour and pollinosity similar to head; apparent coloration also influenced by muscle insertions beneath transparent cuticle and usually by pinkish pigmentation. Mesopleuron, pteropleuron, pleurotergite and upper margins of sternopleuron and hypopleuron pinkish, this pigmentation sometimes extended to haltere (knob), upper margin of subscutellum, entire scutellum and lateral margins of mesonotum posterior to region of transverse suture; unpigmented regions of thorax sometimes with transparent cuticle. Muscle insertions sometimes confer darker and more striking yellow colour on mesonotum, producing broad median (sometimes divided along mid-line) and paired lateral vittae; these vittae may be virtually contiguous. Pleuron also sometimes with similar muscle insertions on lower parts of sternopleuron, hypopleuron, pleurotergite and subscutellum. Legs nearly always entirely yellow, femora occasionally brownish in greasy specimens and tarsi sometimes paler. Haltere usually pale, but knob dark brown in greasy specimens. Wing with striking brown patterning over anterior two-thirds (Fig. 2); cell r_1 with 2 hyaline streaks at and just beyond insertion of vein R_1 on costa, the latter streak (and rarely the former) extending across vein R_{2+3} and usually reaching vein R_{4+5} just distad of crossvein r-m (basad in case of more basal streak); hyaline streaks in cell r_{4+5} distad of r-m nearly always sharply angled near vein R_{4+5} (more basal streak sometimes apically rounded and apical streak sometimes extended into cell r_{2+3}); apical parts of cells r_{2+3} and r_{4+5} appearing predominantly brown infuscate, the former cell conspicuously so. Abdomen variably colored, ranging from yellow to irregularly dark brown, although nearly always with overlay of pinkish pigment, segment 8 and terminal abdominal structures usually paler than more basal segments.

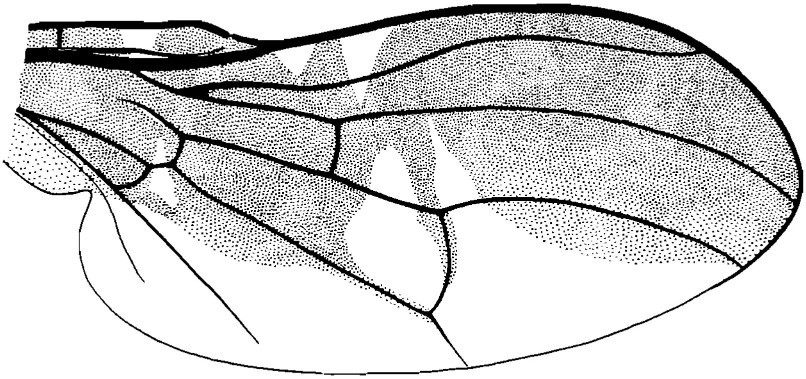
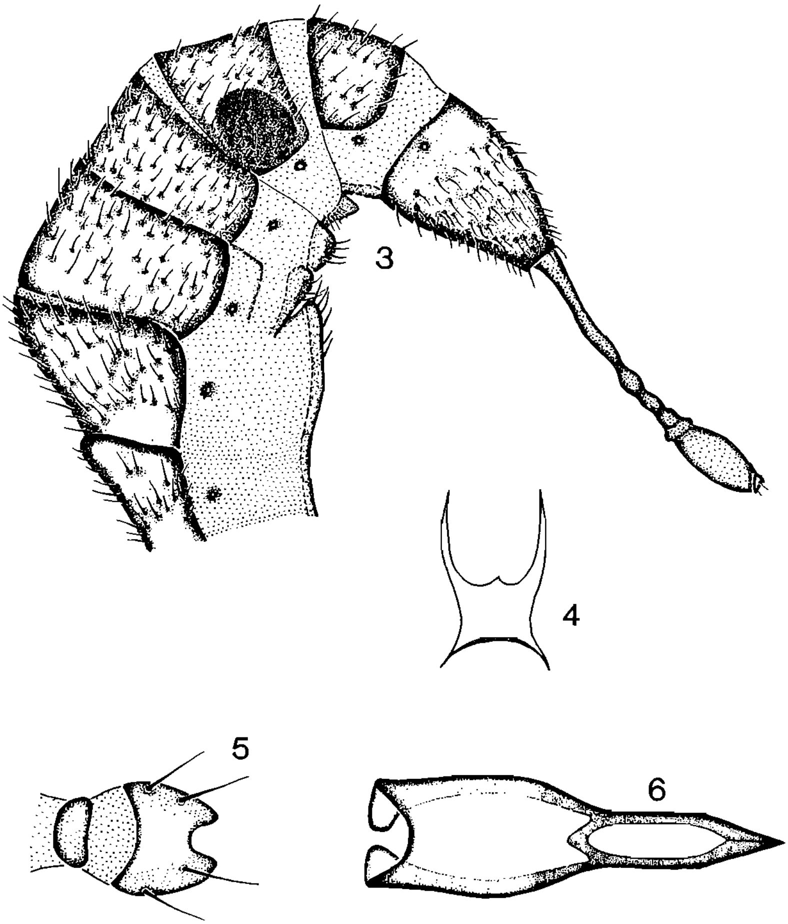


Fig. 2. *Ramuliseta lindneri* Keiser, 1952, wing venation and patterning.



Figs 3–6. Female abdominal/postabdominal characters of Ctenostylidae and Pyrgotidae. 3–5. *Ramuliseta lindneri* Keiser, 1952 (Ctenostylidae). 3. Abdomen, lateral view, showing position of spiracles, dark marking on tergite 5 and form of largely membranous postabdomen (possibly with internal first-instar larva in apical region). 4. Sternite 1, ventral view. 5. Tergite 9 and fused cerci, dorsal view. 6. *Pyrgotina antidorcas* Bruggen, 1961 (Pyrgotidae), aculeus, dorsal view.

Head (Fig. 1): Profrons prominent in profile, much more conspicuous than postfrons. Parafacial visible in profile along its entire length. Frons, at broadest point, about 1.3–2.3 X maximum eye width in dorsal view. Eye depth in profile about 1.4–1.6 X antennal length. Antenna inserted about level with eye centre in profile. First antennal segment with inner lobe extended only slightly beyond base of second segment, antennal bases here contiguous or virtually so. Aristal branches originating from common base, 2 or 3 main branches (sometimes not apparent), these dendritically subdivided. Aristal plumosity sparse relative to *R. madagascariensis*, although may appear more profuse apically. Deep excavation absent between lower extent of parafacial and facial ridge. Subcranial margin with short and inconspicuous hairing. Mesofrons usually not elevated medially, short hairing either side of mid-line often directed noticeably inwards. Bristles, if present, short and weak, often unsclerotised and irregularly developed. Single (inner?) vertical bristle often developed, although sometimes on one side only, always shorter than length of third antennal segment. Ocelli not visible, position of vestigial ocellar triangle near upper occipital margin, often with pair of parallel, divergent or even convergent bristles. Posterior fronto-orbital bristles (1 pair) sometimes present (even on one side only), positioned just anterior to ocellars, anterolaterally directed (2 pairs in Ugandan specimens).

Thorax (Fig. 1): Propleuron always with one or more hairs. Mesopleuron with series of bristles/setulae posterior to vertical suture, more strongly developed ventrally. Sternopleuron and pteropleuron each usually with 1–2 short setulae (sometimes more numerous), these generally inconspicuous. Dorsocentral bristles, if present, usually reduced to a single irregularly developed pair. Scutellum with 1 or 2 pairs marginal bristles/setulae only (basals sometimes not developed or bristles developed on one side only), length of marginal bristles/setulae at most subequal to length of scutellum in dorsal view. Hind tibia with distinct curvature at about basal third, here narrowed to at least half apical width.

Wing (Fig. 2): Costa with striking outward curvature just prior to subcostal break. R_1 not noticeably sinuous, much closer to costal margin along apical half. Anal cell with posterodistal corner receded and smoothly rounded.

Abdomen (Figs 3–5): Sternite 1 not clearly X- or V-shaped, basal margin slightly arched, approximately basal half weakly sclerotised across much of surface, this sclerotisation also extended along lateral margins, although sharply tapered anteriorly (Fig. 4). Tergite 5 with dark metallic spot revealed by clearing with lactic acid, positioned anteroventrally on each side, longest diameter in vertical plane (Fig. 3). Cerci fused, although more heavily sclerotised along lateral margins, each half with two short setulae (Fig. 5). Spermatheca(e) and/or ventral receptacle not evident, despite careful dissection.

Male: Unknown.

Immature Stages: Fresh material was unavailable for study, although comments can be made about eggs and first-instar larvae discovered inside abdomens. Females from South Africa and Tanzania were dissected. Abdominal contents contained mainly first-instar larvae (200–400), although eggs, sometimes with emergent first-instars, were also seen. First-instar larva (South African female): obvious, sclerotised cephalopharyngeal skeleton present, mouthhooks well developed but not as conspicuous or downcurved as in *Lochmostylia lopesi* Keiser; anterior extremity of larva quite sharply tapered, otherwise of about same width in dorsal view along much of length; body apparently membranous except for sclerotised extreme dorsal and ventral parts of each segment; nine segments each with anteroventral band of short spinules (comprising 2 rows), the last band just prior to anus; well-sclerotised, hemispherical, shield-like structure positioned dorso-terminally above anus, posterolateral extremities extended as acutely angled protuberances; short pair of terminal structures visible above anus and below shield-like structure, although posterior spiracles not discernable.

Material examined: UGANDA: 1 ♀, Bwamba (H?), vi.1948, van Someren (BMNH); 1?♀, Bwamba Pass (west side), Ruwenzori Range, xii.1934 – i.1935, F. W. Edwards, 5500–7500 ft (BMNH); 1♀, Fort Portal, Ruwenzori Range, 4.xii. 1934, F. W. Edwards (BMNH). TANZANIA: 3 ♀, Makoa, 10.i.1959, 16.i.1959, 7–27.i.1959, Lindner, Lichtfang (= light-trap) (SMNS). SOUTH AFRICA: *Transvaal*: 1 ♀, Zoutpb. dist. (= Soutpansberg District), vi.1920, H. C. Breyer (NMSA); 4 ♀, Fanie Botha Nat Res, nr Tzaneen, 23°50'S:30°10'E, 2–6.iii.1986, B. Grobbelaar, light trap (NMSA, SANC). *Transkei*: 1 ♀, Port St Johns Dist, 20–25.xi.1961, B. & P. Stuckenberg, at m.v. (= mercury vapour) light (NMSA).

Discussion: Southern African material of *Ramuliseta lindneri* comprises only specimens collected in Transkei and the eastern/northern Transvaal province of South Africa. Absence of the genus from Natal is unexpected, particularly given that collection of Diptera has been relatively intensive there. *Psila* Meigen (Psilidae), previously unrecorded from southern Africa (there appear to be at least three species in NMSA), is also absent from Natal, with comparable distributions in Transvaal and Transkei, but also present in the eastern Cape. The reason for these disjunct distributions is unknown and needs further investigation.

All specimens, except that from Soutpansberg, were taken at light (usually mercury vapour) traps. It is thus assumed that *lindneri* is crepuscular or nocturnal, this probably accounting for its rarity in collections. The Port St Johns specimen was collected in early evening, shortly after dark (Stuckenberg 1963*a*). Pyrgotidae are well known to have similar flight habits. It is not known whether the other two *Ramuliseta* species are also crepuscular or nocturnal.

Pinkish pigmentation is variably present in *lindneri*, ranging from completely absent to conspicuously present on the head, thorax and abdomen, and even the wings. This, coupled with variable states of greasiness, dramatically effect the ground colour of the fly. As it appears almost certain that *lindneri* does not feed, pinkish pigmentation must be inherent, possibly a by-product of a metabolic process. I have not previously seen similar pigmentation in acalyptrate Diptera, although Stuckenberg (1963*a*) stated that it occurs in Cecidomyiidae. It appears not to occur in *madagascariensis* (not mentioned in original description).

Intraspecific variation in the development of bristles is marked in *lindneri*, and there is a tendency for many bristles on the head and thorax to be reduced or absent; these are better developed in the NMSA specimen of *madagascariensis*. Paired bristles are sometimes developed on one side only. Bristles effected by reduction include the fronto-orbitals, ocellars, inner verticals, sternopleurals, dorsocentrals and marginal scutellars.

Abdominal form of *lindneri* is comparable to that of *madagascariensis*, and both species have the dark, anterolateral spot on tergite 5. Unlike *madagascariensis*, however, sternite 1 is not X- or V-shaped (see description). There is also a subtle difference in the development of the fused cerci, which are more heavily sclerotised in *madagascariensis*.

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I wish to thank Dr H.-P. Tschorsnig (SMNS) for the loan of the holotype of *Ramuliseta lindneri* and other assorted specimens of this species from Tanzania. Dr M. Mansell (SANC) kindly donated two specimens of *lindneri* to the Natal Museum collection. Dr B. Stuckenberg, Dr J. Londt and Mr A. Whittington (all of the Natal Museum), and Dr D. K. McAlpine (Australian Museum) critically reviewed earlier drafts of this paper. I am grateful to the Foundation for Research Development (FRD) for continued financial assistance and to Miss K. Duxbury (Entomology Department, Natal Museum) for assistance with artwork.

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